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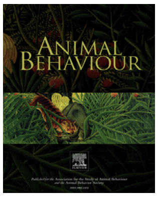

To buzz or burst-pulse? The functional role of Heaviside's dolphin, *Cephalorhynchus heavisidii*, rapidly pulsed signals

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Four groups of toothed whales have independently evolved to produce narrowband high-frequency (NBHF) echolocation signals (i.e. clicks) with a strikingly similar waveform and centroid frequency around 125 kHz. These signals are thought to help NBHF species avoid predation by echolocating and communicating at frequencies inaudible to predators, a form of acoustic crypsis. Heaviside's dolphins produce NBHF echolocation clicks in trains and often in rapid succession in the form of buzzes. In addition, a second click type with a lower frequency and broader bandwidth was recently described, typically emitted in rapid succession in the form of burst-pulses. We investigated the relationship between buzz and burst-pulse signals and both surface behaviour (foraging, 'interacting with the kayak' and socializing) and group size, using a multivariable regression on the signal occurrence and signal count data. Signal occurrence and counts were not related to group size in the regression analysis. Burst-pulses were strongly linked to socializing behaviour, occurring more often and more frequently during socializing and much less during foraging. Buzz vocalizations were not strongly linked to a specific behaviour although there was some evidence of an increase in production during foraging and socializing. In addition, individual level production rates of buzzes during foraging and socializing, and burst-pulses during socializing decreased with increasing group size. Temporally patterned burst-pulse signals were also identified, often occurring within a series of burst-pulses and were directly linked to specific events such as aerial leaping, backflipping, tail slapping and potential mating. Our findings suggest Heaviside's dolphins have a more complex communication system based on pulsed vocalizations than previously understood, perhaps driven by the need to facilitate the social interactions of this species.

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In the animal kingdom, sound serves as a very effective communication modality and often plays a crucial role in species' daily activities including social interactions. Several taxa of birds and a few groups of mammals have demonstrated vocal production learning to develop complex acoustic repertoires which are involved in intraspecific communication (e.g. Janik & Slater, 2000; Naguib, Janik, Clayton, & Zuberbuhler, 2009), while many other vertebrates either cannot or are presumed to do so to a very limited degree (Petkov & Jarvis, 2012). Species that are constrained by a limited vocal repertoire may still use the same vocalizations in different behavioural contexts, leading to context-dependent meaning in vocalizations (Janik & Slater, 2000; Seyfarth & Cheney, 2010). Understanding how highly social species communicate with limited repertoires provides insight into how social interactions can be mediated by context-dependent communication.

Odontocetes (toothed whales) rely on sound for gaining information about the underwater environment (Au, 1993). All odontocetes are presumed to echolocate, by which they emit highly directional biosonar pulses (i.e. clicks) to aid orientation and locate prey during foraging (Au, 1993; Tyack, 2000). Echolocation is generally based on click production, while acoustic communication between animals is facilitated through a variety of either low- to mid-frequency tonal signals including whistles (Tyack, 1986), or pulsed signals such as burst-pulses (isolated series of rapidly produced clicks; Lammers, Au, Aubauer, & Nachtigall, 2004) and codas

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(patterned click series by sperm whales, *Physeter macrocephalus*; Watkins & Schevill, 1977a).

At least 13 odontocete species from four distinct clades echolocate and probably communicate using ultrasonic narrowband high-frequency (NBHF) clicks, which contain most energy above 100 kHz (Au, 1997). These include all members of the *Cephalorhynchus* genus as well as the Kogiidae (two species), Phocoenidae (four species), Pontoporiidae (one species) and some members of the genus *Lagenorhynchus* (two species) (for a review see Morisaka, 2012). Current literature supports the ‘acoustic crypsis’ hypothesis (Andersen & Amundin, 1976; Morisaka & Connor, 2007) which states that NBHF species evolved to favour an echolocation and communication system above the hearing limit of their main predator, the killer whale, *Orcinus orca*. Species that use NBHF clicks appear to have lost the ability to whistle or produce other tonal sounds (May-Collado, Agnarsson, & Wartzok, 2007; Morisaka, 2012; Morisaka & Connor, 2007); however, exceptions have recently been reported for Commerson's dolphins, *Cephalorhynchus commersonii* (Reyes-Reyes, Tossenberger, Iñiguez, Hildebrand, & Melcón, 2016) and franciscana dolphins, *Pontoporia blainvillei* (Cremer, Holz, Bordino, Wells, & Simoes-Lopes, 2017). In general, NBHF species are constrained by a relatively fixed repertoire of pulses; thus, communication complexity is limited (Fischer, Wadewitz, & Hammerschmidt, 2016). However, modification through alterations in click repetition rate could enable a more complex communication system (Clausen, Wahlberg, Beedholm, DeRuiter, & Madsen, 2010), thereby potentially increasing the options for mediating social interactions with sound.

Like many odontocetes, some NBHF species (Martin, Gridley, Elwen, & Jensen, 2018; Sørensen et al., 2018; Yoshida et al., 2014) produce at least two types of fast click series, commonly termed buzzes and burst-pulses, both of which are rapidly pulsed signals with very short interclick intervals (ICI). In bats and odontocetes, a buzz is characterized as a rapid increase in the repetition rate of clicks emitted by an actively echolocating animal, generally linked to the final stage of prey capture (Griffin, Webster, & Michael, 1960; Miller, Pristed, Møshl, & Surlykke, 1995). A burst-pulse is defined as a discrete, isolated series of high repetition rate clicks produced at a relatively constant rate. Burst-pulses are commonly considered to have an intraspecific communicative function (e.g. Lammers et al., 2004) as they are frequently recorded during excited states such as courtship, aggression, aerial displays and immediately preceding distinct changes in surface behaviour (e.g. Blomqvist & Amundin, 2004; Dawson, 1991; Dudzinski, 1996; Herzing, 1996; Simard, Mann, & Gowans, 2008). NBHF species are thought to communicate acoustically with burst-pulses during social encounters (Amundin, 1991; Clausen et al., 2010; Dawson, 1991), where specific click repetition rates and signal amplitude may encode important contextual information related to motivational state such as aggression or may act as contact calls between closely associated individuals such as mothers and their calves (Clausen et al., 2010; Sørensen et al., 2018).

The study of rapidly pulsed acoustic sequences in cetaceans is in its infancy, and the functional role of repeated or patterned pulsed signals in most odontocetes is poorly understood. However, burst-pulse sequences have been reported in several species including bottlenose dolphins, *Tursiops truncatus* (Overstrom, 1983; dos Santos, Ferreira, & Harzen, 1995), northern right whale dolphins, *Lissodelphis borealis* (Rankin, Oswald, Barlow, & Lammers, 2007), Pacific white-sided dolphins, *Lagenorhynchus obliquidens* (Henderson, Hildebrand, & Smith, 2011), white-beaked dolphins, *Lagenorhynchus albirostris* (Simard et al., 2008), dusky dolphins, *Lagenorhynchus obscurus* (Vaughn-Hirshorn et al., 2012) and Atlantic spotted dolphins, *Stenella frontalis* (Dudzinski, 1996; Herzing, 1996). Such reports indicate burst-pulse signals may be used in communicative exchanges or may indirectly broadcast signaller emotion to nearby listeners (Townsend & Manser, 2013).

This study investigated the vocal behaviour of Heaviside's dolphins, an NBHF species endemic to the Benguela upwelling ecosystem along the west coast of southern Africa. Limited information exists on the acoustic emissions and behaviour of this species. Watkins, Schevill, and Best (1977b) recorded four Heaviside's dolphins temporarily held in a rock pool and despite a limited recording bandwidth of 10 kHz, reported click trains and fast click series (500 clicks/s) termed ‘cry’ sounds. Morisaka et al. (2011) reported that Heaviside's dolphins produce typical NBHF clicks with a root mean square bandwidth (BW_{RMS}) around 15 kHz and a centroid frequency (F_C) around 125 kHz with little to no energy below 100 kHz. More recently, Martin et al. (2018) showed that Heaviside's dolphins produce four pulsed signal types, including broadband click trains (median: $F_C = 111$ kHz; $BW_{RMS} = 28$ kHz) and broadband burst-pulses (median: $F_C = 120$ kHz; $BW_{RMS} = 27$ kHz). Acoustic modelling has suggested these broadband burst-pulses can be heard over a much greater area than standard NBHF signals; therefore, they may play an important role in social cohesion of this gregarious species (Martin et al., 2018). However, a socioecological trade-off exists as these signals should be audible to predatory killer whales (Szymanski et al., 1999).

The principal objective of this study was to gain insight into the function of Heavside's dolphin vocalizations by investigating the link between observed surface behaviour and rapidly pulsed signals. Additionally, we examined a subset of burst-pulses composed of patterned pulse configurations and linked these with specific behavioural events to investigate their possible function.

METHODS

Field Site and Data Collection

Data were collected from wild, free-swimming Heaviside's dolphins located in Shearwater Bay, Namibia (-26°37′S, 15°05′E). Shearwater Bay is a small (6.5 km^2), north-facing bay protected from the predominant southerly winds in the area, with a maximum depth of 12 m. Daily recording sessions took place between 0800 and 1400 hours when Heaviside's dolphins were observed from shore and weather conditions permitted (i.e. Beaufort sea state ≤ 2). Acoustic recordings were collected across a range of group sizes, compositions and behavioural states using the following protocol. When one or more dolphins were sighted, an observer situated on board a 4.2 m fibreglass ocean kayak approached the group slowly to minimize disturbance. A visual survey group-follow with incident sampling protocol (Altmann, 1974; Mann, 1999) was used to record surface behavioural states and associated events along with group size, group spacing, presence of nonadults and the estimated distance from the hydrophone array. The small body size and fast movements of this species coupled with the low kayak-based observer platform made it difficult to assess age-related group composition with confidence, so this was not formally analysed. These data were recorded continuously through an audio track spoken by the kayak-based observer. Throughout data collection, a group was defined as two or more dolphins in close association and generally carrying out the same activity. Behavioural state and event definitions were adapted from Henderson, Hildebrand, Smith, and Falcone (2012; Table 1). In comparison to behavioural states, events are relatively instantaneous movements, which were defined as a specific behaviour only when observed with confidence. As the kayak-based observer was restricted in visual range due to a low vantage point, a second survey team visually tracked the kayak and associated dolphins from a land-based vantage point (20 m elevation and

Table 1

Description of surface behaviour categories adapted from Henderson et al. (2012)

Behavioural state	Behavioural events and descriptions
Foraging	Variable direction of movement by individuals within the group Generally remain in same area but can be spread out May have high arching dives, leaps or bursts of directed swimming Visible fish chasing and/or tossing
Interacting with kayak	Individuals or group approach kayak in an investigatory manner and swim closely around it and/or make passes beneath it
Milling/Rest	Variable direction of movement by individuals within the group Remain in one area in close proximity Slow swimming speeds No surface-active behaviour or long dives; stay near surface
Socializing	Possible variable direction of movement by individuals within group Individuals in close proximity, often touching and rubbing Frequent surface-active behaviours including leaps, tail slaps, body slaps, backflips and spy-hops
Travelling	Move in same direction, steadily or rapidly White water and leaping often present during moderate and fast speeds Often synchronous and frequent surfacing

approximately 50 m—1 km from the kayak). Land observers recorded environmental data and monitored the overall presence of cetaceans in the bay. Two-way radios were used to communicate between the kayak-based and land observers to help the former maintain visual contact with focal groups.

Throughout follows, acoustic recordings were made using two high-frequency recording hydrophones (SoundTrap 300 HF; Ocean Instruments, Dunedin, New Zealand) mounted 1 m apart and suspended 1.5 m below the kayak. Only data from a single hydrophone were analysed for this study. Sound was recorded at a sampling rate of 576 kHz with a 16-bit resolution, and the hydrophone settings were configured to include high gain (+12 dB) and a high pass filter (400 Hz) resulting in an effective sensitivity of -171 dB re 1 V/μPa and a flat frequency response from 400 Hz to 150 kHz ± 3 dB. SoundTraps contain an anti-aliasing filter at 150 kHz, resulting in a −6 dB roll-off per additional octave in frequency. Recordings were stored as compressed 30 min SUD files from which WAV files were extracted for subsequent analysis.

Assigning Acoustic Signals to Surface Behaviours

Following Henderson et al. (2011), the recordings were first divided into 30 s segments starting from the beginning of each recorded focal follow. Behavioural data were assigned to each respective 30 s segment of the acoustic data. In cases where no behavioural data were available for a specific 30 s segment, but the preceding and following segments were the same behavioural state, we interpolated the behavioural data across the missing intermediate time segment. However, where two or more consecutive segments had missing behavioural data, these data points were discounted from further analysis. Lastly, 30 s segments containing behavioural information were filtered by distance to the focal group, and only segments containing recordings made within a visually estimated 50 m range of dolphins were selected for further analysis.

Acoustic signals produced by Heaviside's dolphins were identified through visual inspection of the spectrogram display in Adobe Audition CC (Adobe Systems Inc., San Jose, CA, U.S.A.) and were indexed by signal type based on Martin et al. (2018). Martin et al. (2018) defined three distinct groups of Heaviside's dolphin pulsed signals: (1) click trains: series of clicks with ICI exceeding 10 ms composed of either NBHF or broadband click types; (2) buzzes: click series with ICIs < 10 ms and preceded by a slower ICI click train; and (3) burst-pulses: isolated series of high repetition rate clicks that generally begin, persist and end with ICIs < 10 ms (Fig. 1). All distinguishable click series (further referred to as pulsed signals which refers to the entire vocalization) were indexed, except standard NBHF echolocation click trains, which were too numerous to be counted and often overlapping. Instead, we recorded the presence or absence of NBHF click trains in 30 s segments that contained any other pulsed signal type. For each 30 s segment, the occurrence (presence or absence) and number (counts) of broadband click trains, buzzes and burst-pulses were documented. If a pulsed signal overlapped consecutive 30 s segments, it was assigned to the segment in which it began.

Statistical Analysis

A multivariable regression (generalized linear mixed model, GLMM) approach was used to investigate the relationship of surface behaviour and group size with each pulsed signal type using R version 3.4.2 (R Core Team, 2013) and the packages ‘lme4’ (Bates, Mächler, Bolker, & Walker, 2014), ‘glmmTMB’ (Brooks et al., 2017) and ‘DHARMa’ (Hartig, 2018). Surface behaviour was modelled as a categorical predictor and the logarithm ($\log_2$) of group size as a quantitative predictor. We hypothesized that group size may mediate the relationship between surface behaviour and signal production; therefore, an interaction term between behaviour and group size was included.

Based on the study design and evaluation of the data, we recognized that the distributions of counts of pulsed signals had particularly large numbers of observed zeros, termed ‘zero-inflated’. A hurdle model is a type of GLMM that deals with zero-inflated data and is applicable to clustered count data with excess zeros (Mullahy, 1986). A hurdle model involves two random model processes shaping the response. For these data, a binary model examined the presence or absence of a pulsed signal in each 30 s segment, and in those segments for which signals were present, a zero-truncated abundance model determined the conditional distribution of the counts of pulsed signals, per pulsed signal type. The presence or absence of pulsed signals was modelled as a binomial distributed response variable with a logit link function. Depending on the dispersion parameter (residual deviance/degrees of freedom), counts of pulsed signals were fitted as truncated Poisson or truncated negative binomial distributed response variables with a log link function. A normally distributed random intercept was included in both processes to account for nonindependence of segments from the same focal group encounter. To account for potential temporal autocorrelation within encounters, a segment-specific random effect was also included in both processes and

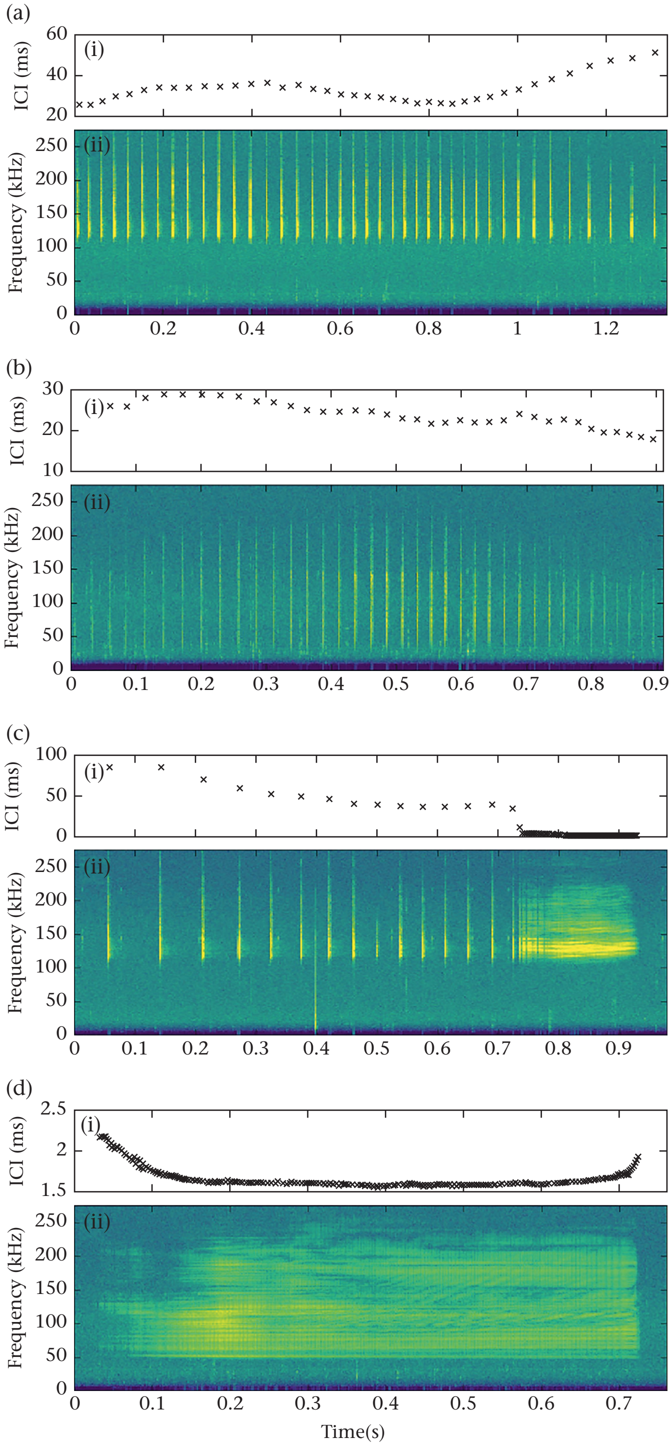

Figure 1. Heaviside's dolphin pulsed signal types: (a) narrowband high-frequency (NBHF) click train, (b) broadband click train, (c) buzz and (d) burst-pulse call. For each signal, (i) the interclick intervals (ICIs) throughout the pulsed signal and (ii) the spectrogram of the signal (512-pt, FFT, Hamming window, 50% overlap, 576 kHz sampling rate; MATLAB version 2017b) are shown.

modelled to follow a continuous time autoregressive process within each encounter because there were often pauses between segments containing pulsed signals.

Residual diagnostic plots with normalized randomized quantile residuals were used to assess model fit and assumptions, and correlation tests and plots of the lagged residuals for up to 10 lags were assessed for temporal autocorrelation. Models accounting for autocorrelation were compared to those not adjusting for autocorrelation by using Akaike's information criterion (AIC) (Akaike, 1973). The main relationship of interest is that between surface behaviour and rapidly pulsed signals. However, we accounted for the possible need to control for group size as well as the modification of behavioural effects by group size. We used likelihood ratio tests (LRT) to test for the effects of group size and removed this variable and the interaction of surface behaviour with group size when there was a lack of evidence for them. Effect sizes are reported as odds ratios (OR) in binomial model components and as incidence rate ratios (IRR) in count model components to assess changes in the response associated with changes in predictor variables. OR and IRR are expressed as ratios relative to a reference category. Preliminary data exploration indicated that broadband click trains were not adequately represented in the data for analysis, and subsequently our quantitative analysis focused on rapidly pulsed signal types (buzzes and burst-pulses).

Pulsed Signal Production Rates

We explored possible group size effects, such as a reduction in individual level production rate in larger group sizes, for buzzes during foraging and burst-pulses during socializing, as these are the behaviours under which they were most commonly expected to occur. Data evaluation revealed an unexpected number of buzzes recorded during socializing behaviour; therefore, this comparison was also included in our analysis. Pulsed signal production rates were calculated by offsetting the count data by group size (i.e. count/group size) per 30 s segment. Production rates were calculated with the original zero-inflated count data as well as the nonzero count data. As large group sizes (> eight individuals) were rare, we truncated the data set and investigated group size effects for groups of one to eight animals for foraging, and two to eight animals for socializing, as no socializing behaviour was recorded for lone individuals.

Patterned Burst-Pulses

Inspection of rapidly pulsed signals recorded from Heaviside's dolphins revealed some unexpected complexity in the temporal configuration, with some burst-pulse signals composed of different configurations of pulses (Fig. 2). Temporally patterned burst-pulse signals were easily distinguished from discrete burst-pulses due to the very short time intervals (generally < 20 ms) occurring between the segments of a patterned burst-pulse compared to the longer intervals occurring between discrete burst-pulse signals. The identified patterned burst-pulse signals were verified as those occurring on recordings from both hydrophones to reduce the possibility of misclassifying a signal as patterned due to off-axis effects on a single hydrophone. Only signals that appeared patterned and with a similar signal-to-noise ratio (SNR) on both hydrophones were included in the analysis. The temporal patterning was assessed manually using the waveform display of Adobe Audition CC and then further verified with a click detector in MATLAB version 2017b (The MathWorks Inc., Natick, MA, U.S.A.; see Martin et al., 2018 for methods), which calculated the amplitudes and ICIs of all signals present. We considered the signals to be emitted from the same animal when consecutive signal amplitudes were similar and ICIs within a segment were regular and stereotyped with the other segments present. If overlapping clicks belonging to other click series were present, these were easily identified by differences in amplitude and ICI and were manually deselected in the click detector.

Through visual inspection, we assigned these temporally patterned burst-pulses to six categories based on broad patterns in

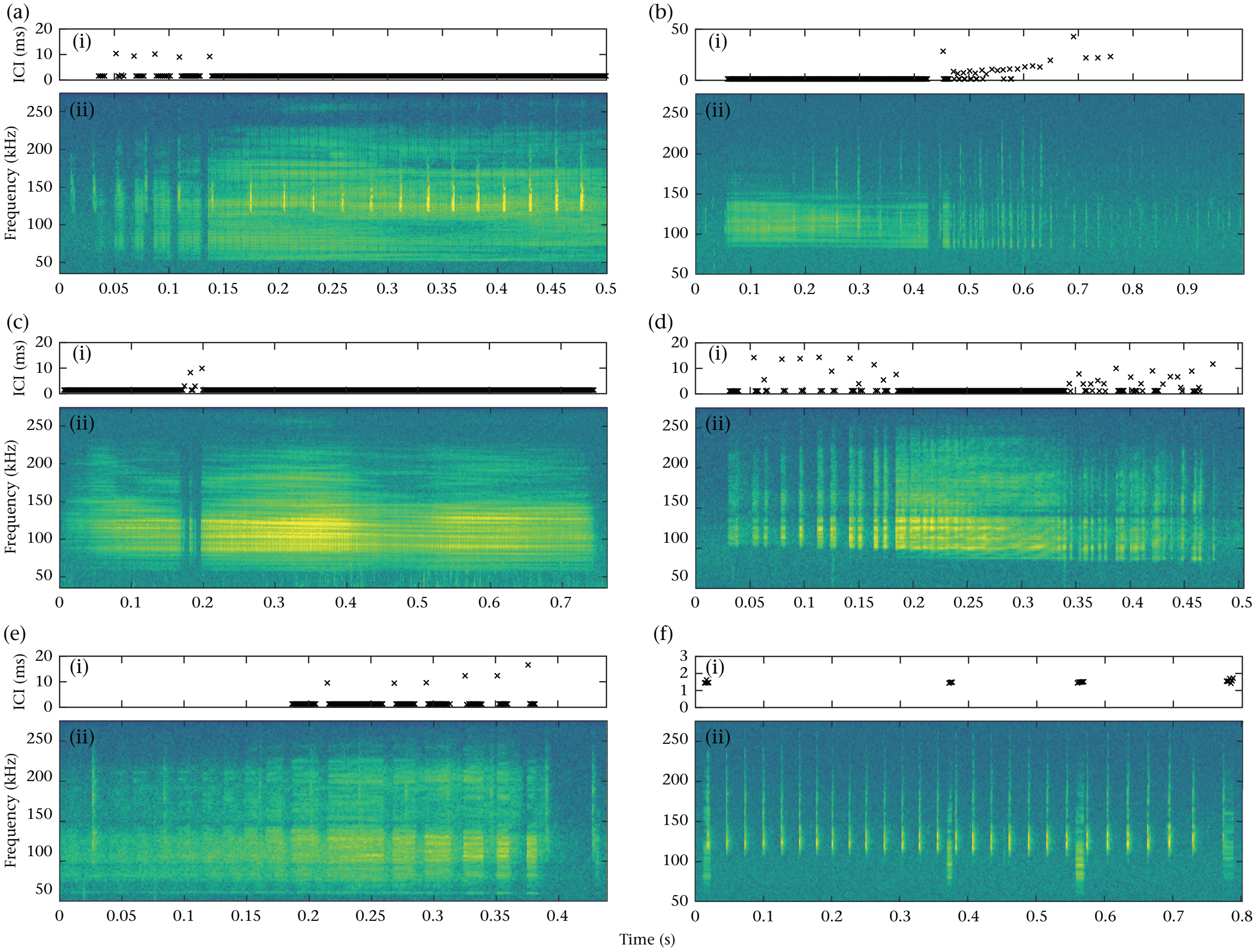

Figure 2. Examples of Heaviside's dolphin temporally patterned burst-pulse signals. (a) Patterned at the beginning, (b) patterned at the end, (c) patterned in the middle, (d) patterned at both the beginning and the end, (e) continuous segmented pattern and (f) series of four short burst-pulses. For each signal, (i) the interclick intervals (ICIs) throughout the pulsed signal and (ii) the spectrogram of the signal (512-pt, FFT, Hamming window, 50% overlap; MATLAB version 2017b) are shown. NBHF click trains from other individuals can be seen overlapping the patterned signals in all spectrograms except in (c) and (d). Note only the latter half of the continuously segmented patterned signal shown was suitable for click detection.

the configurations of the shorter segments of pulses within each signal: patterned at the beginning preceding the main nonpatterned portion of the signal; patterned at the end following the main nonpatterned portion of the signal; patterned in the middle of the signal; patterned at the beginning and end of the signal; patterned throughout the signal; and discrete short burst-pulses (i.e. 'click packets', short signals or series of short signals composed of <12 clicks per signal; Fig. 2). Additionally, we counted the pulses per short segment and the number of segments in conjunction with the main nonpatterned portion of each signal. When behavioural data existed within ±5 s of a patterned burst-pulse signal, a behavioural state and event were assigned to it. Low sample sizes precluded further statistical analysis; therefore, we only describe different temporal configurations in patterned burst-pulse signals linked with behavioural information where applicable.

Ethical Note

This research was conducted by the Namibian Dolphin Project with permission from the Namibian Ministry of Fisheries and Marine Resources and with ethics clearance from the University of Pretoria Animal Use and Care Committee (Reference: ec061-09 AUCC). This research was based on focal animal sampling where dolphins were observed from a distance and not touched or harmed in any way during data collection. Data were collected from a kayak which is considerably quieter, less polluting and less disturbing than motor boats typically used for this type of research. In addition, observer presence was minimal as focal animal sampling was carried out for a total of 25 h on 12 days spread over 2 months. The number of encountered individuals varied by day, generally with fewer than 15 individuals encountered per day.

RESULTS

We collected 25 h of acoustic recordings from wild Heaviside's dolphins located in Shearwater Bay, Namibia. Data from 33 focal groups were suitable for analysis from 10 of the 12 sampling days. Recording sessions lasted between 20 min and 4 h 12 min. Of the 1373 sampling segments identified, 836 were associated with a behavioural observation, and, of these, 347 segments contained at least one pulsed signal (broadband click train, buzz or burst-pulse). In total 93 broadband click trains, 515 buzzes and 774 burst-pulses were identified in these segments, all of which contained NBHF echolocation clicks. No other cetaceans were sighted or detected acoustically during recording sessions, and due to the unique features of the bay (i.e. small mouth, <12 m depth) and secondary observer platform, it is highly unlikely there were other cetacean species in the area.

NBHF echolocation clicks were ubiquitous throughout the recordings while other categories of pulsed signals were less common. Modelling focused on the patterns of occurrence and counts of rapidly pulsed signal types over the behavioural categories in which they occurred. The most frequent behaviours observed were foraging (43.1%), followed by interacting with the kayak (27.5%) and socializing (18.1%). Other behaviours occurred less frequently (travelling 7.6%, mixed socializing 2.4%, milling 1.3%) and we chose not to include these in the analysis. Limiting modelling to only foraging, interacting with the kayak and socializing behaviours further reduced the sample size to 741 segments (Table 2, Fig. 3). These data were recorded over a range of group sizes (1–15 animals, median = 3, mode = 2; Figs. 3 and 4) and group compositions (adults only, multiple adults with a single juvenile, or mother and juvenile pair). No neonatal calves were encountered during this study, and all dolphins presumed to be nonadults based on size are hereafter referred to as 'juveniles'.

Our analysis examined the use of rapidly pulsed signals over three behavioural states. Foraging and socializing behaviours were modelled against interacting with the kayak as the reference behaviour, since the occurrence of buzz and burst-pulse signals were equally distributed in this behavioural category (Table 2). Hurdle model results were generally robust to small changes in model specification. There was some indication of temporal autocorrelation when analysing residuals, and the lowest AIC values were obtained by including the continuous time autoregressive process; hence, final models did include the random effect for temporal autocorrelation. As units of analysis required a behavioural observation to occur within a given segment, there were variable numbers of continuous and discontinuous 30 s segments within each encounter, which may also have assisted with reducing autocorrelation.

Burst-pulses were strongly associated with surface behaviour, but the interaction of surface behaviour with group size and group size alone were not retained as predictors in the final model (LRTs: $P = 0.307$; $P = 0.655$). Burst-pulses occurred most frequently when Heaviside's dolphins were socializing (Table 2), with a 444% increase in the odds of a burst-pulse occurring compared to when dolphins were interacting with the kayak (Table 3). When a burst-pulse was present during socializing, there was some evidence the count rate also increased compared to when dolphins were interacting with the kayak (Table 3). When foraging, the odds of a burst-pulse occurring reduced by 89%, and when a burst-pulse was present, the count rate was also reduced by 86% compared to when dolphins were interacting with the kayak (Table 3).

For buzz data, the interactions of surface behaviour with group size and group size alone were not retained as predictors in the final model (LRTs: $P = 0.190$; $P = 0.574$). Multivariable analysis could not confirm a relationship between surface behaviour and buzz occurrence (P values > 0.50); however, in segments that contained at least one buzz, there was evidence of a possible increase in the number of buzzes recorded during foraging and socializing, compared to when dolphins were interacting with the kayak (Table 3).

Pulsed Signal Production Rate

To investigate evidence of reduced vocal output by individuals when group sizes were larger, we examined group size corrected production rates (count of pulsed signals per dolphin, per 30 s segment) for foraging (buzzes) and socializing (buzzes and burst-pulses), both including and excluding 30 s segments containing no pulsed signals. As few burst-pulses were recorded during foraging (Fig. 4), this relationship was not examined. Buzz rates for foraging groups were highly affected by zero inflation and there was no trend across group sizes (Fig. 5a). However, in the nonzero count data, buzz rate per dolphin gradually declined with increasing group size during both foraging and socializing (Fig. 5b). An increase in buzz rate during foraging was observed at a group size of eight; however, this might have been influenced by low sample sizes for this group size bin (Fig. 3). Analysis of burst-pulse production during socializing indicated a reduction in output per individual animal as group size increased and this result was apparent in both the zero-inflated and nonzero count data (Fig. 5).

Patterned Burst-Pulses

We recorded 35 burst-pulses with patterned configurations and an additional seven arrangements of short burst-pulses (individual or series). In total, 28 patterned signals were recorded within ±5 s of a behavioural observation, of which 20 were suitable for measuring ICI and the number of clicks per segment (Table 4). There were 18 signals recorded during socializing behaviour, nine during interacting with the kayak and one during travelling (Fig. 6). Patterned signal configuration type varied within and across behaviours. For those signals recorded during socializing, the most frequently observed behavioural events were aerial leaps and tail slaps (Table 4, Fig. 6). Overall, patterned burst-pulses were recorded infrequently compared to nonpatterned burst-pulses, and no identical patterned configuration of pulses was found among the analysed signals (Table 4).

Table 2
Summary of Heaviside's dolphin group composition and pulsed signal presence according to surface behaviour

Behaviour	Overall distribution	Group composition			Pulsed signal type		
		Mother with juvenile	Group with juvenile	Adult group	Buzz	Burst-pulse	Broadband click train
Foraging	48.6 (360)	1.7 (6)	12.2 (44)	86.1 (310)	27.2 (98)	8.1 (29)	0.0 (0)
Interacting with kayak	31.0 (230)	14.8 (34)	48.2 (111)	37.0 (85)	24.8 (57)	26.5 (61)	4.4 (10)
Socializing	20.4 (151)	2.7 (4)	11.9 (18)	85.4 (129)	43.7 (66)	68.9 (104)	20.5 (31)

The overall percentages (and numbers in parentheses) of analysed 30 s segments per behaviour category are shown under 'Overall distribution'. The percentages (and numbers in parentheses) of 30 s segments per behaviour category are presented for dolphin group composition and pulsed signal type. Juveniles included all dolphins presumed to be nonadults.

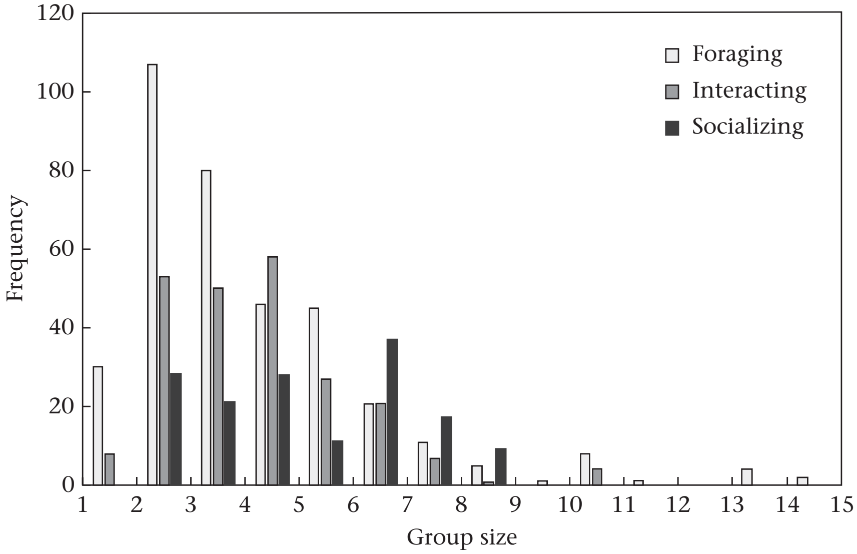

Figure 3. Distribution of analysed 30 s segments ($N = 741$) by group size and surface behaviour category.

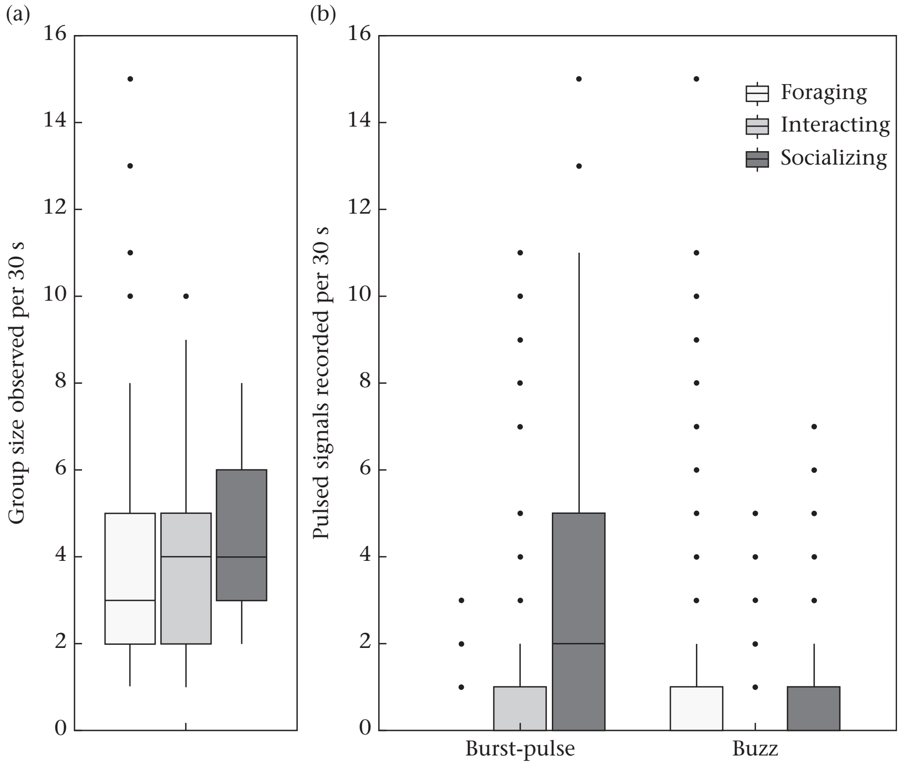

Figure 4. (a) Group size of Heaviside's dolphins and (b) counts of recorded buzzes and burst-pulses by surface behaviour category. The box plots show the median and 25th and 75th percentiles above zero; the whiskers indicate the values within 1.5 times the interquartile range and the circles are outliers.

DISCUSSION

This is the first study to investigate the relationship between Heaviside's dolphin surface and acoustic behaviour. Our results indicate patterns in the behavioural context of sound production, with Heaviside's dolphins probably using pulsed signals produced with different temporal and spectral characteristics to fulfil communicative and foraging functions.

Multivariable analysis confirmed that surface behaviour is related to the occurrence and number of burst-pulse signals produced by Heaviside's dolphins. Burst-pulse signals were most likely to occur, and were produced in significantly higher numbers, when dolphins were socializing compared to other behavioural states (Table 3), supporting the proposed use of burst-pulses as a mode of communication among conspecifics (e.g. Blomqvist & Amundin, 2004; Clausen et al., 2010; Dawson, 1991; Herzing, 1996). However, the nature of what is being communicated remains unclear and our data were restricted to relatively coarse observational states at the group level. Understanding the function of burst-pulses is complicated by ambiguity in the valence of the

Table 3
Hurdle model results for comparison of the occurrence and counts of rapidly pulsed signals between ‘interacting with the kayak’ behaviour and all other behaviours

Predictors	Buzz			Burst-pulse		
	OR/IRR	CI	*P*	OR/IRR	CI	*P*
Occurrence model						
Surface behaviour						
Foraging	0.84	0.48–1.48	0.555	0.11	0.04–0.32	**<0.001**
Socializing	1.11	0.58–2.12	0.751	5.44	1.57–18.79	**0.007**
No. of segments	741			741		
Count model						
Surface behaviour						
Foraging	1.47	0.87–2.47	0.152	0.14	0.06–0.35	**<0.001**
Socializing	1.66	0.96–2.88	0.069	1.39	0.98–1.97	0.063
No. of segments	221			194		

Occurrence of pulsed signals was modelled as a binomial distributed response variable with a logit link function. Counts of pulsed signals were fitted as truncated Poisson (buzzes) or truncated negative binomial (burst-pulses) distributed response variables with a log link function. Effect sizes with 95% confidence intervals (CI) are reported as odds ratios (OR) in binomial model components and as incidence rate ratios (IRR) in count model components. Values based on $P < 0.05$ are shown in bold.

socializing behavioural state, which can be either emotionally positive (e.g. affiliative behaviour) or negative (e.g. aggression) and can include actions that may fall into both categories (e.g. mating). Furthermore, the ultrasonic vocalizations, rigid facial expressions and similar physical characteristics of Heaviside's dolphins combined with poor water clarity make assigning vocalizations to individuals difficult. Noninvasive acoustic recording tags, which also contain depth sensors and accelerometers for orientation (Johnson & Tyack, 2003), offer a method to link sounds to specific behaviours, if they can be successfully attached to the animals (Sakai, Karczmarski, Morisaka, & Thornton, 2011).

For most Heaviside's dolphin burst-pulse signals, the broader bandwidth and lower frequency parameters reduce the directionality and increase the transmission range, potentially up to five-fold in comparison to standard NBHF signals (Martin et al., 2018). Therefore, regardless of signaller intention, burst-pulses are likely to transmit further and be detected more readily by conspecifics than NBHF signals. This supports burst-pulse function as a possible contact call between dispersed group members (Clausen et al., 2010; Ford, 1989; Sørensen et al., 2018). Martin et al. (2018) suggested Heaviside's dolphins relax the strict limitations of acoustic crypsis to increase communication range primarily with burst-pulse signals, while remaining acoustically cryptic when navigating and foraging. However, the features of burst-pulses that improve transmission also make their use potentially costly, as these signals can be heard by predatory killer whales (Martin et al., 2018; Szymanski et al., 1999).

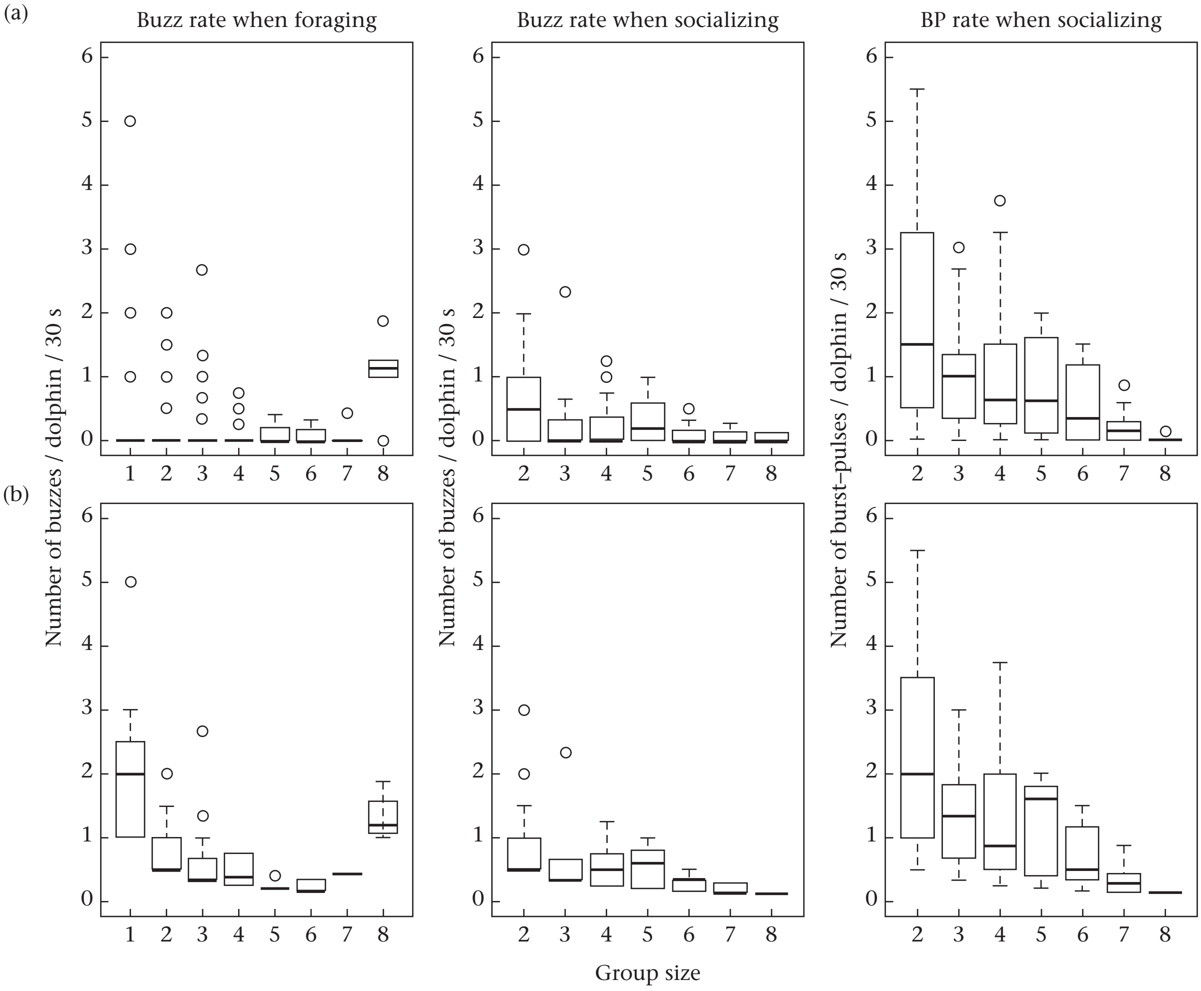

Figure 5. Production rates of Heaviside's dolphin buzzes recorded during foraging and socializing behaviours and burst-pulses (BP) recorded during socializing behaviour across group sizes. (a) All analysed segments (including signal counts of zero) and (b) presence only (nonzero) count data. Group size is truncated to a maximum of eight individuals. The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the circles are outliers.

Table 4

Description of Heaviside's dolphin temporally patterned burst-pulse signals with paired surface behavioural states and events for signals that were measurable ($N = 20$)

State	Event	Patterned type	Pulse count
I	Around kayak	Beginning	4+5+5+6+9+12+BP
I	Not defined	Beginning	2+2+4+1x4+BP
I	Approach kayak	Beginning	1x7+2x10+3+4+6+BP
I	Around kayak	Middle	BP+3+6+BP
I	Around kayak	End	BP+4+1+2+1+1+3+1x3+2+1+2+1+2+1+2+1+1+2+1+2+1x3+2+1+2x5+1
I	Bubble cloud	Short	6+9
S	Leap	Beginning	1+2+11+BP
S	Leap	Beginning	2+7+2+2+3+2x3+3+4+1+4+2+4+BP
S	Leap	Beginning	1+3+3+1+4+3+2+BP
S	Tail slap	Beginning	1x29+2x8+3+3+4+5+8+BP
S	Splash	Beginning	1+3x6+2+1+2+1+2x4+3+4+3+BP
S	Tail slap	Beginning & End	7+4+3x5+4+3+3+4+BP+2+1+3+2x3+6+5+2+5+1+1+3+6+1
S	Leap	End	BP+1+1+3+2x3+1x8
S	Tail slap	End	BP+6+2+1x19
S	Mating	Segmented	(Unidentified segment)+16+34+14+15+11+7+5
S	Splash	Short	6+6+12+4+5+4+4+9+7+5+4+4+3+3+2+2+3+3+5+7+7+4+5+5
S	Skid	Short	7
S	Rapid tail slaps[a]	Short	4
S	Rapid tail slaps[a]	Short	7+5+8+9
T	Swims away	Short	6+8

I: interacting with the kayak; S: socializing; T: travelling. Pulse count represents the number of pulses per segment, with segments separated by a '+' symbol. 'BP' represents the main nonpatterned portion of the signal. A multiplication symbol 'x' followed by a number represents the number of times identical segments were repeated in a specific section of the signal. For example, a pulse count of 4+1x4+BP = 4+1+1+1+1+BP, where there are five segments containing either one or four pulses per segment leading up to the main nonpatterned portion of the signal.

[a] Event where the dolphin's body was flexed horizontally at the surface while rapidly tail slapping the water's surface.

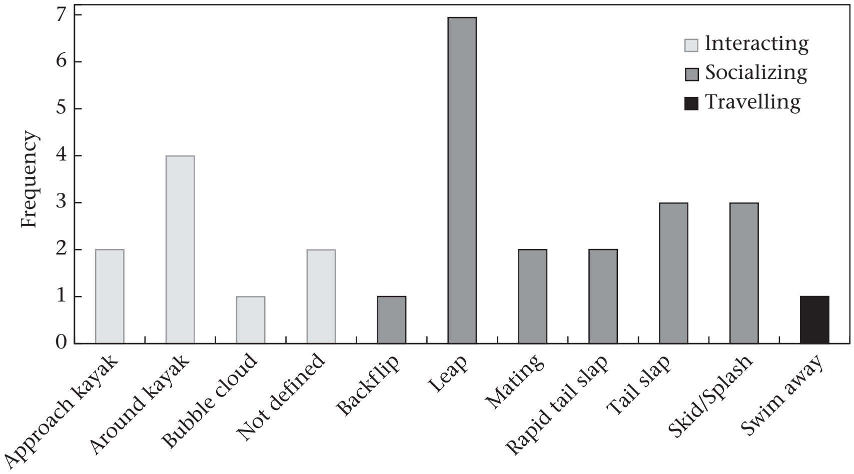

Figure 6. Distribution of Heaviside's dolphin temporally patterned burst-pulse signals that were paired in time (±5 s) with an observed behavioural state and event.

For species constrained by a relatively fixed repertoire of only pulsed signals, adding unique components (e.g. modifications in click repetition rate) to otherwise similar signals can give rise to a moderately open-ended system of communication (Clausen et al., 2010; Seyfarth & Cheney, 2010). For those delphinid species that lack whistling capabilities, burst-pulses may encode context-specific information including potential individual or group identification as suggested by Rankin et al. (2007).

Odontocetes are capable of vocal production learning, and social learning of specific pulse repetition rates has resulted in group-specific dialects in killer whales (Ford, 1991) and sperm whales (Weilgart & Whitehead, 1997). Heaviside's dolphins are generally found in small group sizes, but occasionally aggregate into groups of 20 or more individuals (Behrmann, 2011). Although difficult to study in detail due to low levels of individual distinctiveness, Heaviside's dolphins live in a dynamic fission–fusion society and appear highly social (Behrmann, 2011; Elwen, 2008). Like other social odontocetes (Gero, Whitehead, & Rendell, 2016; Janik & Sayigh, 2013; Tyack, 2008), communication using individually distinct acoustic labels might be expected. However, consistent distinct patterns in burst-pulse signal structure (e.g. pulse repetition rate, duration or frequency modulation), which would be necessary in this 'acoustic signature' scenario, were not observed. The majority of burst-pulse signals were graded with no clear separation of distinct types (Marler, 1976; Murray, Mercado, & Roitblat, 1998), and there was limited support for stereotyped burst-pulse production that would be necessary to communicate individual or group identity. However, further detailed study of the burst-pulse structure might refine this. Broadly speaking, the production rate of burst-pulses does appear to reflect heightened emotional arousal of the signalling animals (see Briefer, 2012 for review).

Although limited by sample size, we did observe a close relationship between the presence of recorded temporally patterned burst-pulse signals and an observed energetic action by at least one member of the focal group (Table 4, Fig. 6). Patterned signals were recorded on half of the sampling days across seven focal groups, and most were recorded within a series of burst-pulses while animals were socializing and often in conjunction with a specific behavioural event such as aerial leaping or tail slapping (Table 4, Fig. 6). It is possible that patterned burst-pulses cue or follow specific behavioural events, a finding that suggests underlying complexity not fully accounted for within the graded communication explanation. We suggest this with the caveat that these signals may be influenced by variations in signal propagation caused by rapid animal movements; therefore, further research is necessary to confirm whether temporally patterned burst-pulse signals are true components of Heaviside's dolphin acoustic repertoire.

For buzz data, multivariable analysis could not confirm a relationship between surface behaviour and buzz occurrence, but in segments that contained at least one buzz, there was evidence of a possible increase in the number of buzzes recorded during foraging and socializing compared to the reference behavioural state (Table 3). As in bats, an odontocete buzz signal starts during the transition between the initial and terminal approach stage of prey capture (Griffin et al., 1960; Madsen, Johnson, de Soto, Zimmer, & Tyack, 2005; Miller et al., 1995). Dolphins in this study were not observed underwater, and prey capture attempts were not seen, so all foraging-related behaviour was placed in a broad behavioural state that encompassed both searching and prey capture events. This resulted in the buzz data being highly zero-inflated during foraging which reduced the ability to confidently link buzzes to specific states. During times when fish were observed at the surface, high numbers of buzzes were recorded from the focal group, supporting the functional use of buzzes to aid in prey capture as described in other odontocetes (e.g. Arranz et al., 2016; Johnson, Madsen, Zimmer, de Soto, & Tyack, 2004; Madsen, de Soto, Arranz, & Johnson, 2013; Wisniewska et al., 2016).

Odontocetes may use sounds in a multifunctional way such as for foraging and communication. In this study, several buzzes were recorded during socializing and occasional burst-pulses were recorded during foraging (Table 2, Fig. 4). It is possible that dolphins encountered some prey while socializing; however, buzz signals may also serve a social function such as the proposed social buzzes in bats (Schwartz et al., 2007; Fenton, 2013). Burst-pulses recorded during foraging could reflect a cooperative group foraging strategy which has been suggested in other delphinids (Henderson et al., 2011; Vaughn-Hirshorn et al., 2012), or if a burst-pulse directly followed a successful prey capture, it could be a form of excited victory sound (Ridgway, Moore, Carder, & Romano, 2014) or perhaps used to mediate food sharing (Deecke, Ford, & Slater, 2005). Buzzes and burst-pulses commonly co-occurred when dolphins interacted with the kayak (Table 2). Captive Commerson's dolphins emitted buzzes and burst-pulses when new objects were introduced to their tank (Yoshida et al., 2014). Although speculative, the presence of both signal types in each circumstance may indicate that dolphins communicated with burst-pulse signals while acoustically examining the foreign object with buzz signals.

Despite being the most infrequently recorded signal type, at least one broadband click train occurred in 20.5% of analysed socializing segments compared to 4.4% of interacting with the kayak segments, while none were recorded during foraging segments (Table 2). To our knowledge this is the first NBHF species reported to produce broadband clicks in click trains and burst-pulses as adults; however, Reyes-Reyes et al. (2016) reported sporadic broadband clicks from adult Commerson's dolphins. Heaviside's and Commerson's dolphins may use broadband click trains to serve a communicative function rather than for echolocation; however, further studies are required to investigate this.

Our results indicated a decline in individual level production rates of buzzes and burst-pulses with increasing group size. However, buzz rates during foraging and socializing were much lower and more similar across group sizes than burst-pulse rates during socializing (Fig. 5b). These observed differences between buzzes and burst-pulses can be explained at least in part by differences between the two signal types with respect to directionality and source level as well as behaviour affecting the individual animal's aspect relative to the hydrophone. Based on spectral properties, there is potential to record more Heaviside's dolphin burst-pulses than buzzes for any given group because burst-pulses are less directional and travel further underwater (Martin et al., 2018). Several odontocetes have been reported to reduce buzz source level output immediately prior to attempted prey capture (Au & Benoit-Bird, 2003; Jensen, Bejder, Wahlberg, & Madsen, 2009; Wisniewska, Johnson, Nachtigall, & Madsen, 2014), including NBHF species (Akamatsu, Wang, Wang, & Naito, 2005; Gotz, Antunes, & Heinrich, 2010). If Heaviside's dolphins also reduce source level output during buzz production, the active space and detection probability will be reduced further. Additionally, when socializing, Heaviside's dolphins are often closely bunched together and regularly touch other group participants (see definition in Table 1), while when foraging, individuals may be more dispersed and frequently change direction when searching for prey (Aguilar Soto et al., 2008; Arranz et al., 2016; Johnson et al., 2004; Miller, Johnson, & Tyack, 2004). The combination of the high directionality of buzz signals and potential reduction in source level, coupled with higher group dispersion of foraging dolphins, may lead to more missed buzz detections than burst-pulses. Thus, burst-pulses should provide a more accurate reflection of the true number of signals emitted by the group than buzzes.

Heaviside's dolphins produced fewer burst-pulse signals per dolphin in larger groups (Fig. 5), which may help reduce signal masking as observed in bottlenose dolphins (Jones & Sayigh, 2002; Nowacek, 2005; Quick & Janik, 2008). In larger groups, where acoustic signals may be masked, dolphins may switch from acoustic to alternative sensory modalities such as touch or visual cues to communicate information to nearby individuals. Male *Cephalorhynchus* dolphins have saw-toothed serrations on the leading edge of their pectoral fins which have been proposed to be used in sociosexual tactile rubbing (Best, 1988; Gómez-Campos et al., 2010) (Table 1). While further research is required to address this possibility, our findings have key implications for future acoustic monitoring studies of Heaviside's dolphins and other NBHF species, because individual call rates are not constant, but appear to be modulated by group size and behaviour. A comparative study should examine the relationship between NBHF echolocation click trains and group size as this may provide a better representation of individuals present.

Our findings suggest Heaviside's dolphins have a more complex communication system based on pulsed vocalizations than previously understood, perhaps driven by the need to facilitate social interactions as observed in other NBHF species (Clausen et al., 2010; Dawson, 1991). Furthering our understanding of the repetition rate, spectral properties and context of Heaviside's dolphin pulsed sounds may uncover more about their role in echolocation and communication, as both buzzes and burst-pulses at some level appear to be used in different behavioural contexts.

Declaration of Interest

The authors have no conflicts of interest.

Data Availability

The data are available at https://data.mendeley.com/datasets/rvt2byb7px/draft?a=ced7ef2c-717c-43d0-906f-fccf871bb069.

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Supplementary Material

Supplementary material to this article can be found online at https://doi.org/10.1016/j.anbehav.2019.01.007.

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